NOTES ON THE BEHAVIOR OF THE DIMORPHIC ANT *OLIGOMYRMEX OVERBECKI** (HYMENOPTERA: FORMICIDAE)

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Species of the myrmicine genus *Oligomyrmex* are common in tropical Asia, although the ants are easily overlooked because of their small size and inconspicuous activities. The genus is of special interest because of the well developed worker dimorphism shown by all species. Some natural history information is available on *Erebomyrma* (Eidmann, 1936; Wilson, 1962, 1986), the American sister group to *Oligomyrmex* which has only recently been resurrected from synonomy with that genus (Wilson, 1986). However, the natural history of Old World *Oligomyrmex* ants has never been investigated.

I have made preliminary behavioral observations on a colony of *Oligomyrmex overbecki* Viehmeyer collected in Singapore (fig. 1). This species is clearly one of the world's smallest ants, with minor workers having head widths of 0.29–0.32 mm, while the "miniature" majors have head widths of 0.42–0.45 mm.

Materials and Methods

The study colony was collected on the grounds of the Botanic Gardens of Singapore, under bark still firmly attached to the trunk of a large *Eugenia grandis* tree (Myrtaceae), within 50 cm of ground level. The colony was placed in a plastic box 20 × 10 × 7 cm deep, with a moistened paper-mache bottom gouged towards one end with several small, shallow chambers, which were then covered with a sheet of glass. The ants moved into the artificial nest chambers, where they could readily be observed through the glass.

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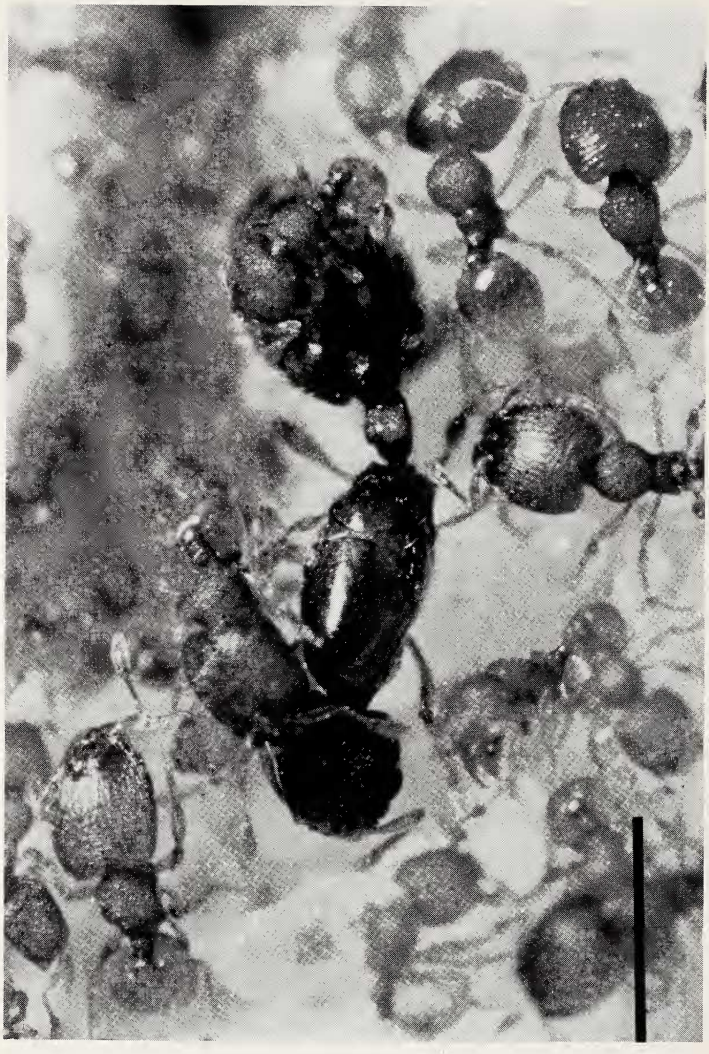

Fig. 1. Portion of *Oligomyrmex overbecki* study colony, showing the queen (center), minor and major workers, and brood. Scale bar = 1.0 mm.

A behavioral repertoire of the workers was compiled during 14 hours within a four day period beginning five weeks after the colony was collected. Estimates of total repertory size were made by fitting the observed behavioral frequencies to a lognormal Poisson distribution as described by Fagen and Goldman (1977), using a computer program supplied by R. M. Fagen. Additional behavioral data was gathered during roughly 25 hours of observations before the repertoire study.

While collecting the repertoire data, light-colored (callow) minors, which were uniformly golden-yellow to light brownish yellow, were distinguished from more darkly pigmented minors (varying from yellowish brown to brown, with antennae, legs and gaster lighter). In addition, the non-callows were subdivided into "repletes," which had their gasters moderately expanded with yellowish fluid, and non-repletes, which had small, contracted gasters. (By this criterion, all major workers and all callow minor workers were judged to be "replete.")

Voucher specimens from the study colony have been deposited in the Museum of Comparative Zoology (Harvard University).

Results

Nesting habits: The workers, queen and brood were tightly massed together between two small adjacent pieces of superficial bark. No food was seen within the nest. The nest area was originally estimated to contain about 400 workers, but upon return to the United States for study, 31 majors and about 180 minors remained. The original proportion of major workers probably approached ten percent.

Repertoire: The complete behavioral repertoire of the worker castes and subcastes is presented in Table 1. During the period in which the worker data was collected, 27 behavioral acts were observed for the queen, including 19 instances of nipping at immatures (described below), five self-grooming events and three instances of licking large larvae. The total repertoire size is estimated to be between 32–36 for the minor caste (data from all subcastes combined), and between 6–11 for the majors (95% confidence intervals).

Table 1. Repertoiries of *Oligomyrmex overbecki* worker castes, including subdivisions of the minor caste (see text). Numbers represent the proportion that each behavior represented of the total number of acts observed for each type of worker.

	Replete Minor	Non-replete Minor	Callow Minor	Major
Self-grooming	0.2443	0.2632	0.2237	0.6074
Allogroom minor	0.1401	0.1219	0.0461	0
Allogroom major	0.0104	0.0042	0.0066	0
Allogroom queen	0.0048	0.0014	0	0
Lick eggs	0.0248	0.0028	0.0921	0
Lick small larva	0.0200	0.0125	0.0066	0.0123
Lick large larva	0.2284	0.1759	0.1645	0.1411
Lick pupa	0.0587	0.0111	0.1974	0.0061
Carry eggs	0.0483	0.0069	0.1908	0
Carry small larva	0.0041	0.0028	0.0197	0
Carry large larva	0.0352	0.0457	0	0
Carry pupa	0.0028	0.0014	0	0
Carry minor worker	0.0035	0	0	0
Pull on queen	0.0014	0	0	0
Nip at immature	0.0076	0.0263	0.0066	0.2209
Assist in:				
larval ecdysis	0.0021	0.0014	0	0
ecdysis to pupa	0.0104	0.0042	0	0
adult eclosion	0.0035	0.0042	0	0
meconium removal	0.0035	0	0	0
Manipulate meconium	0.0193	0.0208	0.0197	0
Remove liquid waste	0.0062	0.0042	0	0
Handle nest material	0.0200	0.0706	0.0066	0
Forage	0.0179	0.1371	0	0
Retrieve solid food	0.0007	0.0014	0	0
Eat solid food	0.0248	0.0180	0	0
Feed on immatures	0.0304	0.0291	0	0
Feed larva solid food	0.0041	0	0	0
Regurgitate to:				
larva	0.0048	0.0028	0.0197	0
minor worker	0.0110	0.0248	0	0.0123
major worker	0.0048	0.0042	0	0
queen	0.0014	0	0	0
Carry or eat				
dead nestmate	0.0007	0.0014	0	0
No. acts observed	1449	722	152	163

The most conspicuous difference between the minor worker subcastes was that darkly pigmented non-repletes formed the bulk of the foragers. The repertoire data indicate several other differences in the frequency of behaviors (differences judged significant when $p < 0.05$ with chi-square test). Callow workers carried and licked eggs with greater frequency than did darker colored minors, but carried large immatures less frequently than did the latter. In comparison to darkly pigmented minors, callows rarely fed on solid foods and rarely allogroomed other workers. They also regurgitated to larvae more often than did the darker subcastes, yet apparently seldom regurgitated to other adult ants (difference in frequencies was not significant in the latter case).

Darkly-pigmented replete minors were intermediate between callow and non-replete minors in the frequencies of performance of many of those behaviors that varied most markedly between the minor subcastes. This suggests the possibility that these minors could be intermediate in age between callow minors (which were consistently replete) and non-replete minors.

Majors rarely foraged. During my observations only four majors were seen outside the nest of the captive colony, and one major was observed on a foraging route near the nest entrance in the field. Major workers apparently only fed by regurgitation.

The *O. overbecki* queen did not attract a large retinue of workers, but commonly one or two minors climbed onto her alitrunk or gaster. In addition, twice I observed replete minors briefly pulling on an antenna or mandible of the queen. Only rarely would a major climb onto the queen, and the density of majors was not noticeably greater near the queen than elsewhere.

Occasionally a major, minor, or the queen briefly appeared to try to grip or bite immatures, most commonly large larvae ("nip at brood" in Table 1). The function of this behavior is unclear, for although consumption of brood by minor workers was common, this biting behavior was most frequently performed by majors and apparently never damaged the immatures.

Larvae fed directly on fragments of insect corpses and from food regurgitated to them by minors.

Foraging Pattern and Diet: During my field observations columns of minor workers extended at least 30 cm from the nest on

the bark of the tree. In captivity, foragers often followed trunk routes at least 3–5 cm long before departing from them to forage singly.

Foraging minor workers fed at crushed fruit flies, fragments of freshly killed cockroaches, honey water baits, and Bhatkar diet (Bhatkar and Whitcomb, 1970). The ants avoided wounded fruit flies, and did not recruite minor and major workers to wounded prey as has been observed for *Erebomyrma nevermanni* (Wilson, 1986).

Soon after most large baits were presented, ants began arriving at the bait using a well-defined route, suggesting an odor trail had been laid down. However, recruitment behavior was difficult to document because of the tiny size of the ants and their weak response to food, even following periods of food deprivation.

Typically food was torn into small pieces and carried into the nest by solitary individuals. Whole dead fruit flies near the nest entrances were sometimes dragged into the nest by groups of 2–5 workers. However, this group transport behavior was poorly coordinated, as workers often pulled in conflicting directions.

Repletes: The *O. overbecki* majors were mildly replete ("semi-replete"), with their gasters never expanding to a size much greater than that of their heads. Moreover, the majors were no more replete than replete minor workers (judging by the volume of the gaster relative to that of the trunk).

Emigrations: Two shifts in nest location were documented in the laboratory. These followed periods of mild stress in which a 60 watt bulb was positioned 25 cm above the glass-covered nest chamber, while an unoccupied shaded chamber was provided 4–5 cm away. Within ten minutes the ants became more active, with darkly pigmented minors and a few majors leaving the nest chambers to explore the nest environs. Gradually more and more workers moved back and forth between the nest chambers and the shaded chamber, until it was clear that a set route had been established. Traffic along the emigration route was relatively steady throughout the period of brood transfer, with the number of ants passing an arbitrary point on the route exceeding 20 per minute.

The first immature was carried out of the nest 50 minutes into the second emigration; the sequence of brood transfer is documented in Figure 2. There was no group transport of immatures and no adult

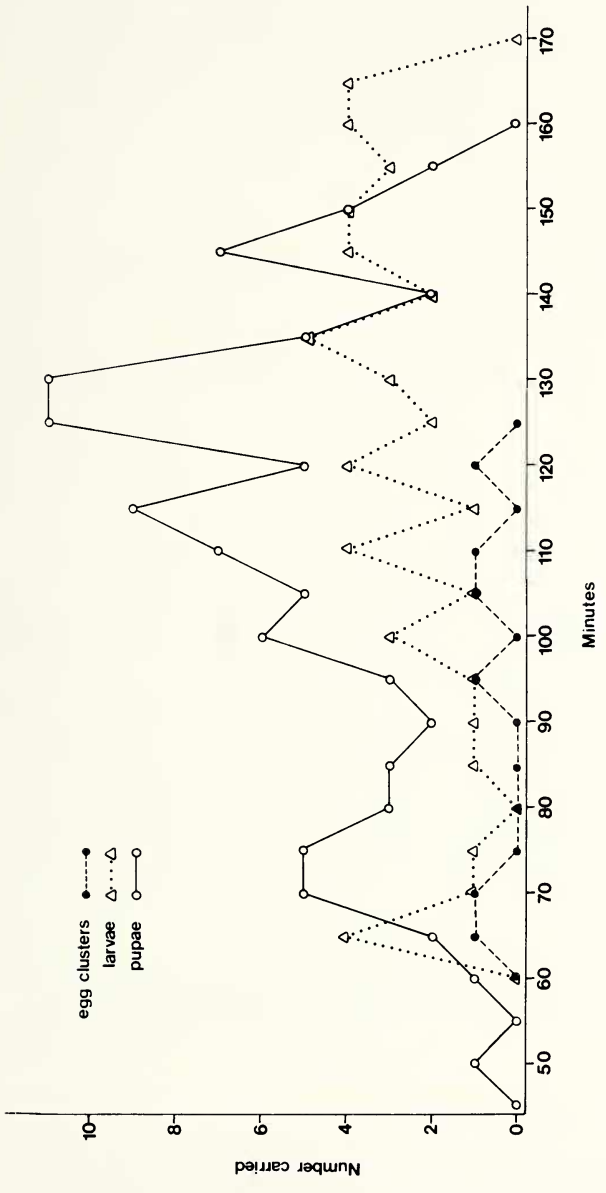

Fig. 2. Transfer of brood during an *Oligomyrmex overbecki* emigration. Times are given as the number of minutes since a strong light was first shined on the ants.

transport (although adult transport of minor workers was observed at other times; see Table 1). Eggs were completely transferred early in both emigrations. The last immatures to be transferred were larvae, not because workers selected pupae over larvae, but because the clumped larvae were difficult to pull apart for transport.

Only minor workers carried brood. Callow minors aided in pulling larvae and pupae free of piles of brood, but were clumsy at carrying larger immatures, which were quickly turned over to darker workers. Callows did, however, occasionally carry small larvae and eggs, taking egg clusters at a higher frequency than did other minors ($p < 0.01$, Fisher's exact probability test). Both replete and non-replete darkly pigmented minors transferred brood, and there were no significant differences between the frequency with which these subcastes carried different brood stages (for each brood stage $p > 0.05$).

The queen emigrated soon after brood transfer began in the first emigration, and ten minutes before the start of brood transfer during the second emigration. She moved rapidly within a small entourage of minors, but no workers rode on her during her journey.

Alarm and Defense: In three trials in which a small *Solenopsis geminata* worker with excised gaster was dropped into the brood area, most workers and the queen fled to adjacent nest chambers, with some minor workers carrying brood. Usually several major workers and a few minors stayed close to the intruder, mandibles open and facing the *Solenopsis*. Sometimes the ants attempted to bite the intruder. As described for *Erebomyrma nevermanni* (Wilson, 1986), the proportion of major workers near the intruder was clearly higher than in the colony as a whole. The ants responded similarly to freshly crushed minor heads presented on applicator sticks, suggesting the head as a source of alarm pheromones. Majors were particularly attracted to crushed minor heads, approaching them with their antennae directed ahead and mandibles open. There was virtually no response to crushed thoraxes and gasters.

Discussion

The major workers of *Oligomyrmex overbecki* apparently function primarily in colony defense and as repletes. The replete condition is very poorly developed (the ants are "semi-replete" in the sense of Wilson, 1986). Major workers also participated to a limited

extent in brood care. It is possible that the repertoire of majors is normally more restricted, but that high minor worker mortality in the captive colony and the resulting altered caste ratios led to an expansion of the major worker repertoire. The relationship between worker caste ratios and major repertoires for dimorphic ants is only beginning to be explored (see Wilson 1984, 1986).

Observations on a *Oligomyrmex* cf. *solidaris* colony collected in a rotten log from Bako National Park in Sarawak indicates that the majors of this species also are semi-replete and are crucial to colony defense. *O.* cf. *sodalis* majors were quick to attack *Pheidologeton silenus* and *Pheidole megacephala* workers dropped into the nest areas, and were much more efficient than minor workers in inflicting damage on the enemy. The importance of rapid and effective response to workers of these ant species was dramatized when the artificial nest container housing the *O.* cf. *sodalis* colony was raided by *Pheidole megacephala* ants. Within a four hour period the *Pheidole* had completely destroyed the *Oligomyrmex* colony of several hundred individuals and emigrated into their nest container.

Minor workers of *O. overbecki* show a pattern of temporal polyethism common for ants (Wilson, 1971), caring for immatures (particularly smaller immatures) as callows and shifting towards foraging activities as they age. Probably only younger workers are semi-repletes, with the ants losing their replete condition at about the time they begin to forage.

Oligomyrmex overbecki (as well as *O.* cf. *sodalis,* pers. obser.) forms trunk trail foraging routes, as do a variety of other pheidologetine ants: *Erebomyrma nevermanni* (Wilson, 1986); *Pheidologeton diversus* (Moffett, 1984) and all other *Pheidologeton* species (pers. obser.); and *Lophomyrmex bedoti* (Moffett, 1986).

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